

ON THE VALIDITY OF *HELICONIUS TRISTERO* BROWER AND
HELICONIUS MELPOMENE MOCOA BROWER, WITH NOTES ON SPECIES
CONCEPTS IN *HELICONIUS* KLUK (LEPIDOPTERA: NYMPHALIDAE)

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Abstract.—Lamas' (1998) criticisms of Brower's (1996a) taxonomy are shown to be based on misinterpretations of the evidence and of the rules of nomenclature. The names *H. amaryllis amaryllis f. bellula* Stichel and *H. melpomene bellula* Turner are unavailable. The name *H. bellula* Brower is available but invalid. The name *H. melpomene mocoa* Brower is the valid name for the subspecies of *H. melpomene* from the Putumayo region of southeastern Colombia. The Genotypic Cluster Species Concept is contrasted unfavorably to the Phylogenetic Species Concept with respect to the aims of systematics in general, and the resolution of relationships among geographically differentiated *Heliconius* taxa in particular.

Key Words: *Heliconius melpomene bellula*, *Heliconius tristero*, nomenclature, circumscription, subspecies

Recently, Lamas (1998) published a critical discussion of two new names applied to *Heliconius* butterflies from the upper Rio Putumayo basin in southeastern Colombia (Brower 1996a). The taxa in question are Müllerian mimics: one (*H. tristero*) was described as a species in the *H. cydno* Doubleday clade, while the other was named as a subspecies, *H. melpomene mocoa*. Most members of the *cydno* clade exhibit blue-and-white or blue-and-yellow wing patterns and mimic species in the *sara-sapho* group (cf. Brown 1981, Brower 1994, and Brower and Egan 1997 for reviews of phylogenetic hypotheses among *Heliconius* species), so it was a surprise to discover a new species mimicking sympatric races of *H. melpomene* (L.) and *H. erato* (L.).

That these formerly conflated taxa represent two distinct entities is supported by

robust evidence stemming from three different sources (mitochondrial DNA sequences, genitalic morphology and wing patterns), and that at least one of them required a new name is not at issue. Lamas' criticisms of my paper focussed on the following problems: (1) the availability of *H. bellula* Stichel (1923); (2) the supposed synonymy of *H. melpomene mocoa* Brower with *bellula* auctt.; (3) my interpretation of the International Code of Zoological Nomenclature (1985) with regard to hybrids; and (4) the logic of my species concept. First, I will address these problems in narrow relation to Lamas' critique of my paper (1996a). My rebuttal of Lamas' criticisms is followed by a brief discussion of the species problem in *Heliconius*. An English translation of the relevant section of Lamas' paper is included as Appendix 1.

REPLY TO LAMAS' CRITIQUE

Is Heliconius bellula Stichel (1923) an available name?

As Lamas (1998) pointed out, Stichel (1923) applied the name *bellula* to a form of *H. amaryllis amaryllis* C. & R. Felder (*H. amaryllis* is now considered to be a subspecies of *H. melpomene*; cf. Ackery and Smiles, 1976). Lamas argued that Stichel's employment of *bellula* was infrasubspecific and therefore formally unavailable. However, Neustetter (1929) cited Stichel's name as a trinomial form of *H. amaryllis*, thus implying that the name was available (ICZN Article 16). The subsequent employment of the name for a geographical race by more recent authors (e.g., Turner 1971, Brown 1979, Sheppard et al. 1985, Mallet 1993, Brower 1996b) further suggests that the name has been treated as available (Art. 45gii), and it was under that premise that I dealt with it in my paper (Brower 1996a)¹.

However, given that Stichel's holotype is not a representative of the *melpomene* clade (see Brower 1996a and below), Lamas' opinion that Stichel's name was quadrinomial provides a convenient excuse to sink it and avoid the complications described above. If its original designation is deemed infrasubspecific, a name remains unavailable until a description is provided (Art. 10c). Lamas claimed that Turner (1971) employed the name *bellula* to refer to a subspecific entity, thereby becoming its author (Arts. 23j and 50c). However, Turner's tentative use of the name in a figure legend (followed by a question mark) was not accompanied by a description. Likewise, Brown (1979), Sheppard et al. (1985), Mal-

let (1993) and Brower (1996b) used the name, but none of them provided a description of the taxon, nor did any of them cite Stichel's description (which would not per se change its availability, in any case: Art. 11dii). All of those uses of *bellula* employ it as a nomen nudum and none of them satisfies the criteria of availability (Art. 13a).

Holzinger and Holzinger (1994) provided a description and illustration of *H. melpomene bellula* and cited Stichel (1923), but their book is not consistently binominal (it uncritically employs numerous infrasubspecific names), and its contents are thus unavailable (Art. 11c). Ironically, it appears that my 1996 paper is the first to provide a description for *H. bellula* that would render it available under all the criteria of Art. 11 (via illustrations, description of differentiating features, identification of a holotype, and citation of Stichel 1923). But because I circumscribed the concept narrowly, to refer to a hybrid form typified by Stichel's original type specimen, the name is invalid. Even so, my definition prevents subsequent usage of *bellula* for any other *Heliconius* taxon (Art. 23h; see hybrid section, below). Thus, the correct authorship of *Heliconius bellula* is Brower (1996a), but the name does not refer to any valid taxon, regardless of its repeated misapplication in recent works (including my own).

Subjective synonymy of bellula and mocoa?

Lamas (1998) argued that *H. melpomene mocoa* Brower is a junior subjective synonym of *H. melpomene bellula* auctt. Since *bellula* is not a valid name, this is a moot point, but it raises another important issue: Lamas' claim shows that has been deceived by Müllerian mimicry! It is the holotype of *bellula* and the holotype of *H. tristero* that are closely-related, while the holotype of *H. melpomene mocoa* represents a different clade. Had Lamas examined the relevant characters, he would have seen that *bellula* and *mocoa* are not the same under any reasonable circumscription *H. bellula* (what-

¹ I examined and discussed Stichel's holotypes of *bellula*, *permira* and *degener*. Lamas suggested that I was unaware of four additional forms described by Stichel from the Mocoa region. Rather, these were deliberately omitted from discussion, because it was clear from the original descriptions that they represent various hybrid forms with recombinant wing patterns that are even less similar to the modern "*bellula*" concept than the two other forms I discussed.

ever its status) is not an example of the *H. melpomene* species group; instead, it is close to *H. tristero* in the *H. cydno* species group. To include *bellula* and *mocoa* in the same species, one would have to view *H. cydno* Doubleday as a subjective junior synonym of *H. melpomene* (L.)! I described this problem explicitly in Brower (1996a), and it was precisely the desire to avoid such confusion that prompted me to coin new names for both the *cydno* relative (*H. tristero*) and the *melpomene* relative (*H. melpomene mocoa*) in the first place.

Even if *bellula* and *mocoa* were closely related, it is clear from Stichel's (1923) descriptions (Appendix 2) that he felt that *bellula* was different enough from the local "nominate form" to warrant a separate name. Stichel believed (in error) that his three "typical" specimens were *H. amaryllis amaryllis*, today recognized as a distinct *H. melpomene* subspecies with an allopatric distribution in the Huallaga valley of Peru (Sheppard et al., 1985). Although ideas about what entities within *Heliconius* deserve names have changed as knowledge of phenotypic variation and geographical distribution has grown, efforts to redefine an old name of dubious availability in specific contradiction to its original author's intent seem procrustean. A more reasonable view is that the "nominate form" of *H. melpomene* from Mocoa and environs was anonymous until I (Brower 1996a) named it.

Hybrids and the ICZN

Lamas (1998) also criticized as erroneous my invocation of Articles 1b and 23h to curtail the current usage of *bellula* because its holotype is a hybrid (Brower 1996a). He pointed out that because the definition of "hybrid" in the ICZN glossary states that offspring of crosses between conspecific subspecies are not hybrids, *bellula* cannot be considered a hybrid taxon. Re-examination of Brower (1996a) shows Lamas' point to be technically incorrect: I hypothesized that the *bellula* holotype specimen was the result of hybridization between *H.*

heurippa and *H. tristero*, both of which I explicitly claimed were species in that paper. Under such circumstances ICZN article 23h specifically applies².

Whether or not the *bellula* holotype actually represents a hybrid or not (and which parental species might have spawned it) is difficult to determine in retrospect and without extensive data from experimental genetic crosses. That additional specimens displaying the same pattern have not been collected suggests that the holotype exhibits a rare recombinant wing pattern (typical of the phenotypic diversity found in other *Heliconius* hybrid zones). By contrast, there are multiple specimens from multiple localities that appear very similar to the holotype of *H. melpomene mocoa*, and illustrations of "*H. melpomene bellula*" in recent works (e.g., Turner 1971, Brown 1979, Holzinger and Holzinger 1994) all lack the yellow spots that are present in the *bellula* holotype. My interpretation that the specimen does not represent a "pure" geographical race is complementary to Stichel's (1923) opinion that the *bellula* holotype is transitional, as shown by his description of it as distinct and separate from his series of specimens of the local "nominate" form.

Logical Consistency

I made several statements that Lamas chose to overlook in his conclusion that my taxonomic argumentation (Brower 1996a) "no tiene sustento lógico al ser refutable." First, I did not argue that the current classification of *Heliconius* is not illogical. Indeed, I stated that I chose the ranks I employed to preserve nomenclatorial stability,

² Lamas objected my use of the term "forbid" (translated as "prohibe" in his paper) with reference to the ICZN rule on names applied to interspecific hybrids. Article 23h says, "A species-group name established for an animal later found to be a hybrid . . . must not be used as a valid name for either of the parental species, even if it has priority over all other available names for them, but it may enter into homonymy." I leave it to the reader to contemplate whether "must not be used" and "forbids the use of" mean the same thing, or not.

even though I knew that the species delimitations among geographically polymorphic *Heliconius* butterflies were effectively arbitrary. The final points of my paper were that,

“The mitochondrial DNA data suggest that the degrees of relationship among the *H. melpomene* races and among the *H. cydno* races are similar, and that divergence times within each group are also approximately the same, implying that the taxonomic rank of each group should also be the same. The entire species-level classification of the genus will probably require revision as additional data become available.”

Ignoring these qualifying remarks, Lamas offered (without providing new data or examining the characters discussed in Brower [1996a]) a hypothesis of circumscription that he considered “more valid” than my view: that *H. timareta* Hewitson, *H. heurippa* Hewitson and *H. tristero* are conspecific. He based this notion on these entities’ geographical proximity on the northeastern slope of the Andes, evidence of hybridization among them (which he denied on the following page), and their hypothesized close relationship (based on studies of mtDNA: Brower 1996a, 1996b). However, both the mtDNA studies and data from a more comprehensive recent analysis (Brower and Egan 1997) imply that *H. timareta*, *H. heurippa* and *H. tristero* are no more closely related to one another than any of them is to *H. cydno* or *H. pacheus* Salvin. Therefore, if one wanted to lump diagnostically different taxa based on the symplesiomorphy of potential interbreeding, the logically consistent choice would be to collapse all of these taxa under the oldest species-group name (*H. cydno*). I said as much in 1996a.

If Lamas (1998) were as concerned with the consistent assignment of taxa to the appropriate rank as his criticism of Brower (1996a) implies, then according to his “more valid” hypothesis, he should have

named his new *Heliconius* subspecies (described in the same paper) not “*H. timareta timoratus*, ” but “*H. heurippa timoratus*” (if *timareta* and *heurippa* are conspecific, then the former is either a junior synonym or a subspecies of the latter). Under the interpretation Lamas claimed that he prefers, *timoratus* would seem to be an infrasubspecific form of the subspecies *H. heurippa timareta*! The complexity of sorting out names, ranks and relationships among geographic races in *Heliconius* obviously presents a challenge that neither Lamas nor I have yet resolved in a fully satisfactory manner.

Synonymies

Heliconius melpomene mocoa Brower, 1996a.

Heliconius melpomene bellula auctt. (Turner 1971, Brown 1979, Sheppard et al. 1985, Mallet 1993, Brower 1994, Holzinger & Holzinger 1994) [misidentifications; unavailable name].

Heliconius melpomene mocoa Brower 1996a: 328. Holotype: Colombia, Dpto. Putumayo, 1–3 km N. Mocoa on rd. to Pitalito, 25 March 1992 leg. AVZ Brower. Deposited in Cornell University Insect Collection (examined).

Heliconius heurippa* × *Heliconius tristero, natural hybrid

Heliconius amaryllis amaryllis f. *bellula* Stichel, 1923: 262. Original type specimen: Colombia, Río Putumayo, Río Guayuyaco, 7 July 1921 leg. W Hopp (see Brower 1996a for transcript of original labels).

Heliconius amaryllis f. *bellula* Stichel; Neustetter 1929: 58.

Heliconius amaryllis f. *bellula* Stichel; Brower 1996a [identified as hybrid *H. heurippa* × *H. tristero*].

NOTES ON SPECIES CONCEPTS IN *HELICONIUS*

I suspect that the root of Lamas’ criticisms of my concepts of *tristero* and *mocoa* lies in his concept of species in *Heliconius*,

which differs from mine. The species problem in *Heliconius* has been controversial for many years (e.g., Eltringham 1916 vs. Kaye 1916); indeed, it is the very complexity of geographical diversification within the genus that has led it to become a model system for the study of the evolutionary genetics of mimicry (Sheppard 1960, Emsley 1964, Turner 1971, Brown et al. 1974, Mallet 1993). Many of the *Heliconius* papers from the post-typological period applied the biological species concept (BSC; Mayr 1940)), which unites allopatric taxa based on their potential to interbreed. In recent years, the BSC has been criticized on theoretical and practical grounds, and numerous alternative species definitions have been proposed that offer more operational criteria for species delimitation (Eldredge and Cracraft 1980, Mishler and Donoghue 1982, de Queiroz and Donoghue 1988, Nixon and Wheeler 1990, Baum and Shaw 1995, Mallet 1995). Lamas' critique implied that he favors the "genotypic cluster" species concept (GCSC; Mallet 1995), while I (Brower 1996a) applied the phylogenetic species concept (PSC) as elaborated by Nixon and Wheeler (1990).

Evidence and Criteria of Specific Distinctness

Mallet (1995) argued that the PSC fails to provide "clear guidelines" for dividing species because it recognizes groups based on apomorphy: "With detailed morphology and modern molecular techniques," he asserted, "one can find apomorphies for almost every individual," which he suggested would result in rampant splitting and proliferation of species. This simplistic caricature of the cladistic method misrepresents the procedure of species delimitation, which has been explored in depth by Davis and Nixon (1992), Doyle (1995) and Brower (1999). Cladists identify populations of organisms that they hypothesize to be distinct, and seek discrete differences between them. If they discover such differences, cladists consider the populations to be separate

species; otherwise, they are collapsed into a single species. That the cladistic approach may yield finer resolution of the hierarchical pattern of diversity than alternative methods is considered by many to be an asset. In short, the guidelines of the PSC are clear: it is Mallet's understanding of them that seems cloudy.

Mallet's (1995) alternative, the GCSC, views species as "identifiable genotypic clusters" recognizable by "a deficit of intermediates" at single and multiple loci, and views speciation as "the production of divergent populations that can coexist in sympatry." There are a number of problems with this approach. First, there are no explicit criteria for identification of genotypic clusters. That Mallet employed "deficit" instead of "absence" implies that he believes that the clusters need not be fixed for alternate alleles, but merely differ in allele frequency by some "significant" amount. Further ambiguities include how many markers should be sampled (Mallet [1996] suggested multiple loci), and what should be done if one locus suggests continuity, while another suggests distinction. The across-locus averages that Mallet (1995) employed in the hybrid indices he presented would disguise heterogeneity among loci. A more sophisticated and logically consistent, but equally labor-intensive approach to multilocus species discrimination was presented by Doyle (1995). In practice, however, methods like these that rely on exhaustive characterization of gene pools are rarely employed in the study of biological diversity, because they entail intensive, quantitative sampling that is not feasible in most circumstances.

Another difficulty with the GCSC is non-dimensionality.—Mallet's concept is only useful for contemporaneous taxa in sympatry or parapatry. To cover everything else, Mallet (1995) suggested that "closely related allopatric forms should mostly be considered conspecific." But how are we to determine that allopatric forms are "closely related?" If allopatric populations are

“identifiable,” then they logically satisfy Mallet’s GCSC criteria and are distinct species by definition; if they are not identifiable, then why would we hypothesize that they were different in the first place? When the hypothetical taxa under investigation occur in allopatry, researchers are forced to turn to the empirical comparison of features of organisms to draw inferences about their taxonomic relationships. The PSC recognizes separate species only when fixed differences are discovered between hypothesized groups, which will always result in the recognition of a minimal number of taxa in comparison to methods based on frequency differences. The claim that the PSC oversplits taxa relative to the GCSC is simply false.

In summary, Mallet’s GCSC is a methodologically explicit version of the nondimensional BSC (Mayr 1963). It is labor-intensive, depending upon sampling of multiple individuals at multiple loci to provide empirical evidence of the absence of interbreeding. It bases the decision of specific distinctness on an arbitrary and unstated level of phenetic bimodality in a histogram of average genetic scores. Although Mallet and colleagues have made a rather convincing case for the distinctness of *Heliconius erato cyrba* Godart and *H. himera* Hewitson on the basis of this method (Jiggins et al. 1996), that work represents a laborious multi-year, multi-authored effort to corroborate a conclusion about a single pair of taxa that had already been hypothesized by systematists years before (Descimon and Mast-de Maeght 1984). How Mallet’s concept could be useful in the best of circumstances to a museum taxonomist working with qualitative samples of preserved, dead specimens on pins is not clear. What is quite evident is that Lamas has never employed the GCSC in any of his published taxonomic work, including the descriptions of new subspecies in Lamas (1998). Given this lack of consistency and rigor, it is especially ironic that my (1996a) names should be subject to such scrutiny, when

they are perhaps the most thoroughly-diagnosed *Heliconius* taxa that have been published, the differentiating characters having been drawn from the results of cladistic analyses of mtDNA, and corroborated with diagnostic characters from external and internal morphology (Brower 1996a) and data from a nuclear gene (Brower and Egan 1997).

Recognition and Circumscription of Subspecies

Although the genus *Heliconius* contains numerous diagnosably different populations that bear valid species-group names, most of these are considered to refer to intraspecific variations. Since the rejection of rampant typological splitting in the early 20th Century (e.g., Riffarth 1902), *Heliconius* species have been circumscribed primarily by the BSC criterion of interbreeding. Under that criterion, otherwise uniform parapatric populations that hybridize where they abut have been considered conspecific. Likewise, distinct populations that hybridize with each of two otherwise allopatric neighbors provide a transitive link that has allowed lumping of chains of populations into single, geographically extensive “biological species.” These species’ component “geographical races” are diagnosably different (i.e., they display heritable characters that allow their unambiguous determination), and have been considered by many researchers (e.g., Brown et al. 1974, Shepard et al. 1985, Brower 1996a, 1996b) to represent historically distinct entities. That their names are in common use in the literature and in museum classification schemes is a de facto acknowledgement of their recognition as taxa, even by those biologists who would emphatically deny their specific status. According to the PSC, diagnosably distinct groups that it is useful to name are considered separate species, and every recognized “geographical race” in *Heliconius* should be a phylogenetic species.

The ICZN (Art. 45a) considers names at

both specific and subspecific levels to be labels for taxa of a single category, the Species Group. The concept of subspecies is simply a convenient label for taxa at one of the potentially many hierarchical levels nested within the genus, as revealed by cladistic studies. The Code is sensibly silent on the problems of definition and boundary determination of concepts associated with name-bearing type specimens; such decisions are considered subjective, and left to the judgement of the describer and subsequent employers of the name. In most instances, the older *Heliconius* names were described from one or a few dead specimens in European collections, and were not accompanied by any discussion of the circumscription of the associated concept, beyond designation of an intraspecific level (e.g., subspecies, form, aberration, etc.). A good example of such a perfunctory description is Stichel's original diagnosis (1923) of *H. amaryllis amaryllis f. bellula* (Appendix 2).

Minimal original descriptions leave a great deal of latitude for subsequent interpretation. Such interpretations should strive to maintain nomenclatorial stability, but only when the names preserved are precisely and accurately associated with empirically supported concepts. If a concept diverges from the description due to the acquisition of new specimens and data to the point that the description is no longer adequate, some action is called for, ranging from redescription of the holotype to the separate description of differentiated concepts as distinct taxa. The currently-recognized "geographical races" (= phylogenetic species) of *Heliconius* are taxa corroborated by a century of empirical research in laboratories, museums, and the field. They bear names originally applied to the single holotype or short type series, and to which the current concepts correspond. The focus of modern systematic effort should be on the empirical diagnosis of such taxa and the inference of hierarchical relationships among them, not on empty disputes over

the arbitrarily determined ranks that particular taxa do or do not represent. *H. melpomene mocoa* and *H. tristero* are both diagnosably distinct taxa of the Species Group.

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APPENDIX 1

Translation of Lamas' (1998: 119–120) critique. Translation is as precise as possible, but some idioms were translated freely to improve comprehensibility. For complete literature citations, see Lamas (1998)

Status of Heliconius tristero Brower and *H. melpomene mocca* Brower

Recently, Brower (1996) has described two new taxa of *Heliconius* from Putumayo, southeastern Colombia, based on preliminary data from analysis of

mitochondrial DNA sequences. Both names are discussed separately here.

Heliconius tristero was diagnosed by Brower (1996) as a taxon of the species group, belonging to the *H. cydno* Doubleday clade, and narrowly separated from *H. heurippa* Hewitson and *H. timareta* Hewitson. Although he did not mention it explicitly, Brower seems to imply that *heurippa*, *tristero* and *timareta* could constitute a subclade of the *cydno* group. The three taxa exhibit an allopatric distribution, *heurippa* occurring in the central eastern region of Colombia, *tristero* in southeastern Colombia and *timareta* in eastern Ecuador (and northern Peru, *vide infra*); while *heurippa* and *tristero* (so far as is known) are phenotypically monomorphic, *timareta* is polymorphic. Brower (1996: 330) concluded that "... *tristero* is considered a species only because its geographically adjacent close relatives, *H. heurippa* and *H. timareta*, have been traditionally considered species as well." This conclusion is not so logical as to be irrefutable. A more valid (and refutable) hypothesis would be to consider the three taxa conspecific, based on Brower's own molecular and morphological analyses (which would show their narrow evolutionary relationship), their allopatric distributions (and geographical proximity), and the supposed existence of transitional forms ("hybrids") between *heurippa* and *tristero* (represented by the "type" of *bellula* Stichel, but *vide infra*), which might suggest that, as Mallet (1995) put it nicely in his definition of species as "genotypic aggregations:" "... closely related allopatric forms should mostly be considered conspecific." Naturally, even though it is well known that in the absence of evidence of specific distinctness in sympatry the conspecificity of allopatric taxa is arbitrary, such arbitrariness is certainly less than to assign a taxon to a particular taxonomic level following a "tradition."

In synthesis, there are two opposing taxonomic hypotheses: 1) *tristero* is a taxon at the species level, evolutionarily independent of *heurippa* and *timareta*, with its own historical destiny; or 2) *heurippa*, *tristero* and *timareta* constitute a polytypic species with three geographical races (subspecies) which have the same historical destiny. With the scarce taxonomic and genetic information available at the moment, it is impossible to decide which of these is closer to the truth.

The case of *Heliconius melpomene mocoa* seems much simpler, and here I offer the hypothesis that *mocoa* is no more than a new synonym of *H. m. bellula* Turner, 1971, as I will demonstrate below. The name *bellula* was introduced for the first time in the literature by Stichel (1923), who proposed it as a form of *Heliconius amaryllis amaryllis* C. & R. Felder, thus constituting an infrasubspecific name (excluded by the ICZN). The name *bellula* recently became available when Turner (1971) elevated it to the subspecific level (as a subspecies of *H. melpomene* (L.), making the name attributable to Turner (ICZN Arts. 10c, 23j, 50c).

Brower examined the male specimen upon which Stichel based his infrasubspecific name *bellula* (and which constitutes the holotype of *bellula* Turner) and decided that it represented an individual belonging to the *cydno* clade, and not to *melpomene*. Brower also examined the "holotypes" of two other infrasubspecific names proposed by Stichel (1923), *permira* and *degener* (which have never been elevated to the subspecific level and thus are nomenclaturally unavailable), suggesting that they might represent hybrids between *H. heurippa* and *H. tristero*. What is more, he assumed that the type of *bellula* appeared to be a recombinant backcross between these hybrids and *tristero*. Arguing that the ICZN "forbids" the use of species-level names that are based on hybrids, he decided to set aside the name *bellula* and establish new names for the member of the *cydno* clade (*tristero*) and the subspecies of *melpomene* present in the upper Río Putumayo (*mocoa*).

Brower does not seem to have realized that Stichel (1923), in addition to *bellula*, *permira* and *degener*, described four other "forms" of *amaryllis* from the region of the upper Putumayo (*anacreonitica*, *perrara*, *rufata* and *aglaspis*), and that other authors introduced six additional names for specimens from the same zone (*parva* Neustetter, *temuifasciata* Neustetter, *aurofasciata* Neustetter, *paula* Neustetter, *paulina* Niepelt and *carminata* Niepelt). In my opinion—and contrary to Brower's view—these 13 names pertain to examples of *melpomene*, and represent transitional forms ("hybrids") between the subspecies *bellula* Turner and *malleti* Lamas. All those specimens were captured around Mocoa (01°09'N, 76°37'W) by collectors who worked for Werner Hopp, and were very likely obtained in the hybrid zone near Villa Garzón (= Villa Amazónica; 01°05'N, 76°35'W, 420 m), a site studied by Mallet (1993), a few km. East of Mocoa. The holotype of *bellula* is labeled as having been obtained on the Río Guayuyaco (written "Guagzayaco" on the label), possibly very near the village of Guayuyaco (= Nápoles; 01°04'N, 76°26'W). The other specimens bear the localities Río Mulato (01°08'N, 76°36'W), 500 m; Mocoa, 530 m; or simple "Mocoa" (for a general description of the area, see Salazar 1995). Mallet (1993) referred to the hybrids found near Villa Garzón as the product of the transition between *bellula* and *aglaope* C. & R. Felder; the correct name of the latter subspecies is *malleti* Lamas, since the subspecies *aglaope* is limited to the lower Río Marañón, lower Río Huallaga and the Río Ucayali basin in Peru (Lamas 1988).

Of the 14 names applied to *bellula* × *malleti* hybrids, the "purest" example corresponds to the holotype of *bellula*, which only shows tiny yellow spots at the costal inner edge of the discal red forewing band, appearing almost identical to the holotype of *mocoa* (which lacks the yellow spots). Brower based his judgement on the presence of these yellow spots, and

the morphology of the genitalia of the *bellula* holotype, to assert that that specimen was a *heurippa* × *tristero* "hybrid," (the same as *permira* and *degener*). But, in the first place, *heurippa* (one of the supposed parents) is not known from the Mocoa region, only from much further north, from the Meta and Guayabero basins, while surely *tristero* should occur in the basin of the Río Orteguaza, since *bellula* has been reported from there. (It would be very interesting to discover if *heurippa*, or *tristero*, or both, occur in the Río Caguán basin, between the Guayabero and the Orteguaza). Further, even though Brower admitted that "male genitalia of the taxa examined are similar, and display substantial intra-racial variability in form," he concluded that the genital morphology of the *bellula* holotype corresponded to the *cydno* clade, based on the examination of that one specimen.

Finally, Brower argued that the name *bellula* should be set aside because it is applied to a hybrid (which, as indicated by the discussion above, I consider completely erroneous) and because the ICZN "forbids" the use of names applied to hybrids. In the glossary of the Code (1985: 256) it is clearly indicated that "The progeny of two individuals belonging to different subspecies of same species are not hybrids." The Code does not "forbid" the use of names given to interspecific hybrids, it simply excludes them from nomenclature, except for the principle of homonymy. Therefore, if the name *bellula* does not correspond to an interspecific hybrid, its use to designate a subspecific taxon is perfectly valid, and in consequence, *Heliconius melpomene mocoa* Brower, 1996 is a subjective junior synonym of *Heliconius melpomene bellula* Turner, 1971.

APPENDIX 2

Translation of Stichel's (1923) description of *H. amaryllis amaryllis* and *H. amaryllis amaryllis* f. *bellula* from the upper Putumayo of Colombia.

H. amaryllis amaryllis Feld.

Forma typ.

Two males.—Forewing with a somewhat variable broad red discal patch, somewhat like the figure of *H. amaryllis euryades* Riff. in Gen. Ins. v. 112, plate 3, fig. 10, but with a more blurred distal margin, and which is somewhat indented below the forewing median vein. The yellow transverse band of the hindwing fragmented near the base by thin black lines, and the veins cutting across the band are more or less black. Mocoa (Put[umayo]), September, October.

Among other things, a character of this species is said to be the absence of red basal streaks on the costal margin of the forewing underside. This feature is present in all of the observed nominate and closely allied forms, but based on the other specific characters, particularly the position of the hindwing band, they can only be considered forms of *amaryllis*. This band is somewhat variable, but it is always positioned such that the posterior border lies outside the posterior edge of the discal cell. In a third male specimen (Mocoa, May), the forewing band is somewhat smaller, so that it scarcely touches the end of the cell, the red is faded and greasy, which is often seen as a pathological feature of red-banded *Heliconius*.

Forma *bellula* f. nov.

One male.—Most similar to the nominate form, the crimson forewing patch more ragged on the margin, partly dusted with black scales, the cell almost completely free of red, an additional character is a sulfur-yellow spot proximal to the subcostal vein. The yellow transverse band on the hindwing is broad, extending nearly 7 mm. from the apex to the trailing edge. Hindwing beneath very similar to *H. amaryllis rosina* Bsd. With red basal streaks on the leading edge of the forewing and three red basal spots in the hindwing. Forewing length 41 mm. Río Guaqzayaco (Put[umayo]).